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Effects of Substrate Warming on Sessile Marine Invertebrate Communities in Monterey Bay, California

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EFFECTS OF SUBSTRATE WARMING ON SESSILE MARINE INVERTEBRATE COMMUNITIES IN MONTEREY BAY, CALIFORNIA

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APPROVED FOR THE DEPARTMENT OF MARINE SCIENCE

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ABSTRACT

EFFECTS OF SUBSTRATE WARMING ON SESSILE MARINE INVERTEBRATE COMMUNITIES IN MONTEREY BAY, CALIFORNIA

By Stephen Loiacono

Increasing average global sea temperatures are one of the most direct and alarming consequences of climate change, yet it is still unclear how sessile marine communities will respond in the near- and long-term. In addition, it is unclear if warming ocean temperatures will facilitate marine invasions or primarily benefit native species. To simulate the effects of increasing ocean temperatures on sessile communities, heated settlement plates (n=7) were used in an *in situ* field experiment to investigate how an increase in substrate temperature (2.5°C above ambient) would affect recruitment and community development as compared to unheated control plates (n=9). Experimental treatments were deployed in the municipal harbor of Monterey, California, which was characterized by an assemblage reflecting a mix of native and invasive species (mainly bryozoans, sponges, tunicates, and tube worms). Following three months of community development in the field, heated plates experienced significantly higher rates of initial recruitment, 33% increase in wet weight, increased percent cover of native and invasive species, and an increase of species with both historically southern and northern range limits. This study reinforces the need for *in situ* experimentation to understand the effects of temperature on the dynamics shaping marine communities. *In situ* studies are valuable because they incorporate all ambient factors and are therefore a more reliable predictor for defining the consequences of climate change.

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I want to thank my advisor Dr. Jon Geller for accepting me to Moss Landing Marine Laboratories and providing me the knowhow and means to complete my thesis. I will always remember sitting in the wet lab with Jon for hours identifying unknown invertebrate species under the dissecting scope with the Light and Smith Manual. I was very fortunate to have Dr. Scott Hamilton on my thesis committee as well. Scott's comments were invaluable and allowed me to become a better scientist. I want to thank him not only for his mentorship but his friendship as well. Scott was always a fun, helpful and kind person to engage. I also want to express gratitude to my committee member Dr. Steve Lonhart. Steve allowed me to shadow him on my first dive in Monterey Harbor. The time Steve took to explain the harbor system to me and our talks about biogeography were greatly appreciated and helpful. I will forever be thankful for the guidance of the late Bill Watson and Dr. Kenneth Coale for sculpting me into a better craftsman and fabricator. Bill and Kenneth were essential in the design of my thesis hardware. Steph Flora was also an incredible resource and helped me with MatLab and programming. John Douglas and Jackson Winn were responsible for one of the best working experiences of my life. I want to thank the logistical support from Gary Adams, Billy Cochran, James Cochran, Brynn Kaufmann, and Chris Machado. Lastly, I would like to thank the following people for helping me with my thesis and becoming the person I am today: The Loiacono Family, Maggie, Kevin Cook, Gabriela Navas, Emily and Dharma Dohnam, Angela Szesciorka, Sara Warden, Catherine Drake, Daffy Duck, Christian Denney, Hamilton Fennie, Scotty Gabara, Mike Fox, Paul Clerkin, Drew Seals, James Knuckey, Bobby San Miguel, Bad Religion, Scott Miller, Evan Mattiasen, Peter Parker, The Kaufman Family, and Dana Carvey.

TABLE OF CONTENTS

List of Tables

List of Figures

1.0 Introduction

Significant warming of the Earth's climate due to the anthropogenic burning of fossil fuels is now well established (IPCC, 2007). Models and observations indicate average global temperatures across land and sea surfaces have increased 0.67˚C since the 1900s and will continue to rise at accelerating rates if carbon emissions are not curtailed (NOAA Climate: Global Analysis, 2012). Several studies indicated that a global increase in temperature has adversely affected insect, bird and plant populations, and in some cases, significantly altered the timing and extent of migration (Walther *et al*. 2002, Parmesan *et al*. 2003, Root *et al*. 2003, Thomas *et al*. 2004). Although marine and terrestrial regions are expected to experience thermal changes at different rates, average species range shifts have been greater in the marine community (Burrows et al. 2011).

Although the global trend is for continued warming, temperature change at local levels is predicted to exhibit far more heterogeneity and uncertainty, creating a need to understand effects of temperature change at a finer spatial scale of resolution. For example, a study of native invertebrates in the rocky intertidal of central California reported a significant increase in abundance of species with southern/warm-water origins over species from northern/cold-water habitats (Barry *et al*. 1995). This phenomenon was explained primarily as a consequence of species range shifts in response to climate change, ruling out variables such as El Nino Southern Oscillation and upwelling (Sagarin *et al*. 1999). While some observational studies in the marine environment have examined shifts in species ranges that have been inferred to be caused by warming and climate change (Perry *et al*. 2005, Schultz *et al.* 2011), the majority of experimental studies simulating future climatic conditions in nature have been

limited to either the terrestrial environment or laboratory (Petersen 2011, Scherber *et al*. 2013., Wolfe *et al*. 2013), due to the difficulty of experimentally warming seawater *in situ*. Manipulative studies of ocean warming are needed to better understand the possible consequences of climate variability in natural systems in the hope of aiding resource managers.

Biogeographers often study the shifts in species' range boundaries to better understand the mechanisms that shape species distributions from local to global scales. Past research has indicated that species' ranges can be set by abiotic variables (e.g., temperature, length of the growing season, physical oceanographic boundaries) and biotic interactions (e.g., predator, competition, or mutualist presence/absence or abundance), and that both processes can work in concert (Foran 1986, DeMott 1989, Nedwell and Rutter 1994). In particular, temperature tolerances and energetic requirements are the most widely cited processes that act to set the location of a species' latitudinal endpoints, causing species adapted to warmer waters to stay in equatorial or warm-temperate regions and likewise retaining cold-adapted species at higher latitudes (Bowman *et al*. 2005, Sexton *et al*. 2009).

Climate change has already affected the natural thermal barriers that set historical latitudinal species distributions in the ocean. Reef fishes in the Southern California Bight experienced a 20-year warming period in sea surface temperature (SST) and Holbrook *et al*. (1997) observed a significant shift from a community dominated by cold-water species to that of a community dominated by warm-water species. Likewise, a 40-year study of copepod diversity and species distributions in the Northeastern Atlantic showed evidence of dramatic biogeographic shifts (Beaugrand *et al*. 2002). As SST increased, cold-water copepod species declined in diversity and retreated towards

the poles while southern/temperate species increased in diversity and showed a 10° expansion in their latitudinal range towards the Arctic. Biologists have also used climate models to predict northward, warm-water fish range expansions in freshwater systems based on future temperature predictions for species such as smallmouth bass (*Micropterus dolomieu*) (Sharma et al. 2007), common carp (*Cyprinus carpio*) (Minns & Moore 1995) and the brook trout (*Salvelinus confluentus*) (Rieman *et al.* 1997).

Temperature shifts are known to induce varying ecological and evolutionary changes in community structure through autecological impacts on species traits. Organisms with different tolerances to temperature change will have greater or lesser success as climate warms. Increases in temperature will have harmful effects on any population unable to tolerate or adapt to sudden or abrupt change. For example, Dong and Somero (2009) noted a southern range contraction of the limpet *Lottia digitalis* while the congener *Lottia austrodigitalis* underwent a northern range expansion as temperatures increased. In bivalves, a similar trend was observed between the displaced *Mytilus trossulus* and invader *Mytilus galloprovincialis* (Tomanek and Zuzow 2010). Molecular analysis suggests, in both cases, that temperature tolerance is related to variation in their heat shock protein structures.

Changing temperature regimes can also influence metabolic performance in marine species, depending on species-specific physiological tolerances. Assuming long-term stable conditions, native species' metabolisms should be selected to operate at the most economical level possible for their environment. If the temperature shifts too far from long-term average temperatures, the organism will become stressed causing less efficient metabolic rates and possible mortality (Somero 2002). For example, under laboratory settings, several annelid, bivalve, cephalopod and fish species exposed to

temperatures above their native ranges showed increases in oxygen consumption and heart rates, with an increasing shift towards anaerobic respiration (Pörtner *et al.* 1998, Pörtner & Zielinski 1998, Pörtner *et al.* 1999a, Pörtner *et al.* 2000), clearly an indication of diminishing energy levels. In the previous examples, increasing ambient temperatures consistently reduced the fitness of cold-blooded marine species. Because all species fit along a spectrum of stenothermic (i.e., narrow temperature tolerance) to eurythermic (i.e., broad temperature tolerance), many researchers predict that stenothermic species will be the most negatively affected when a shift in ambient temperature occurs. Thus, identifying which strongly interacting species within ecosystems are steno- or eurythermic will aid in predicting how community structure may change under a warming climate.

As climate change reorganizes communities, biological invasions may increase in frequency (Parmesan and Yohe 2003; Walther *et al*. 2009). The potential explanation for this phenomenon is that successfully introduced species may be more flexible in their physiological tolerances (i.e., eurythermic), and thus better adapted to changing environmental conditions, than native species. Stachowitz et al. (2002) reported a correlation between the recruitment success of three invasive tunicates (*Ascidiella aspersa*, *Botryloides violaceous*, and *Diplosoma listerianum*) and seasonal variation in water temperature over a 12 year period in the Northeastern United States. Recruitment of these invasive species occurred earlier during years where water temperatures were warmer. In addition, Stachowicz et al. (2002) observed growth rates of *B. violaceous, D. listerianum* and the native tunicate *Botryllus schlosseri* under differing thermal regimes in a laboratory setting. Although growth rates of these three species were greatest in the

highest temperature group (21.1-23.3°C), the invasive species had significantly more percent cover than native at this temperature range.

New colonizers will potentially exclude native species through interspecific competition. In Australia, the sea urchin *Centrostephanus rodgersii* expanded its native range south towards Tasmania over the past 40 years (Johnson *et al*. 2011). The range expansion of *C. rodgersii* is currently causing the commercially viable and native blacklip abalone (*Haliotis rubra*) to recede because urchins consume the kelp that provides the drift resource required by the abalone. Unfortunately, it is difficult to predict the ecological consequences of invaders because studies have shown a wide range and spectrum of outcomes, where native/invasive species interactions have been observed to be harmful, benign or even mutualistic (Sax *et al*. 2005).

The vast majority of climate change experiments have occurred in a laboratory setting where temperature manipulations can be conveniently maintained and monitored. Natural recruitment, however, relies entirely on the ambient biota floating in the water column. Therefore, conducting a recruitment experiment in the laboratory can remove unknown species or environmental fluctuations that occur daily. A single previous study in Western Australia experimentally manipulated ocean temperatures *in situ* in a controlled field experiment, by using artificially heated settlement plates. Results indicated that warming resulted in significant differences in community structure, with an invasive ascidian dominating the settlement plates that were artificially warmed (Smale *et al*. 2012). Experimental studies that incorporate the natural environment into their methodological design will often yield more realistic results.

Given the current focus on improving our understanding of the effects of increasing temperature on species ranges, competition, physiology, and recruitment, there is a need to further investigate how anthropogenic changes in climate will alter marine communities. Knowing how the marine biota will react to climate change can assist researchers in understanding the severity of these impacts. Therefore, the goal of this study is to create an *in situ* microclimate in the subtidal zone of Monterey Bay to observe the effects of substrate warming on settlement selection, recruitment dynamics, growth, and community structure in the sessile marine invertebrate fouling communities. Mimicking future climatic conditions will allow for a valuable insight to further understand how biota reacts.

Settlement plates are a useful tool to observe recruitment and community development. The plates provide a surface for primary succession to occur. Due to the challenges of installing and maintaining an *in situ* warming experiment, there are relatively few such experiments compared to the laboratory alternative. Despite these logistical challenges, settlement plates allow for a more realistic study compared to the laboratory setting, which might exclude or introduce an unknown physical or biological factor. Similar to Smale *et al.* (2012), modifications can be made to the plates to alter their temperatures while submerged in the ocean where larvae suspended in the water column can settle. By fitting heating elements to settlement plates, a very localized, small-scale artificial increase in water temperature will occur, which may trigger a response from invertebrate larvae to either settle on the substrate or escape the heat source. Once larvae have settled, the substratum and boundary water temperature increase is expected to affect juvenile life histories. The temperature increase will partially simulate predicted future conditions to study how the local sessile marine

invertebrate community reacts, with a focus on whether native or invasive species will dominate the community on warmed relative to control tiles.

My premise is that a significant increase in ambient temperature will disrupt the typical local community development and successional process, by differentially facilitating settlement, growth or survival by warm-water tolerant and invasive species. I plan to test the two hypotheses listed below. First, experimental plates will show a significant increase in settlement of species that have a southern/warm-water affinity.

I expect to find significantly more fast-growing, thermally tolerant species on the experimental plates than on the controls. The 2°C increase, induced on the experimental plates, will be inhibitory for some, slowing growth rates, but not pass the threshold for mortality. At the same time, other local species will find the 2°C increase beneficial; causing increased growth rates. Therefore, the experimental plates should have a greater biomass over the control plates. The increase in abundance of southern species (i.e. adapted to warmer temperatures) will happen because, in terms of fitness, southern/warm-water species are underperforming under the current conditions in Monterey Bay. The 2°C increase allows for a higher, more ideal, metabolic rate. Northern/cold-water species will not be completely eliminated from the experimental plates, but the 2°C increase will cause a decline in performance by making the environment less ideal for metabolic processes, potentially slowing growth rates or being detrimental to competitive interactions. Second, experimental plates will show a significant increase in settlement of introduced species. While native species have evolved in the recent Monterey Bay temperature regimes, introduced species are drawn from diverse evolutionary backgrounds experiencing slightly to moderately different thermal regimes. Thus, some subset of introduced species may find the changed

climate to be improved and more similar to their source region, while native species are less likely to do so.

2.0 Materials and Methods

2.1 Study System

Monterey Bay, California is located on the Pacific Coast of the United States. Invertebrate species inhabiting the bay experience peak gamete production during the late spring and summer months due to warmer post-upwelling conditions (Farrell et al. 1991, Wing et al. 1995). The southern extent of the bay is home to the Monterey Harbor (Fig. 1), which occurs in the Montereyan biogeographic region, stretching from Monterey Bay to Point Conception, CA (Blanchette *et al.* 2008). The Montereyan region is considered a biogeographic "mixing zone" since northern/cold water, southern/warm water, and cosmopolitan species and invasive species are present. A 2011 field study conducted by the California Department of Fish and Wildlife documented 36 native and 14 introduced species amongst the fouling community in Monterey Harbor (CDFW 2014).

The Monterey Harbor is an ideal location for experimental studies of the processes influencing the development of sessile marine communities because the harbor infrastructure allows for the securing of the settlement plates and hardware to a fixed floating structure. The water motion in the harbor is weak and primarily due to tidal fluctuation, because a concrete sea-wall shields the harbor from heavy wave action. Thus, this location is an ideal place to install hardware and electronics to manipulate temperatures *in situ*.

Figure 1. Location of Monterey Harbor (36.8° N, 121.9° W) in Monterey Bay, California.

2.2 Species Assemblage

Table 1 lists the common species that comprise the fouling community in Monterey Harbor and was compiled by examining data from previous studies (Donat and Winfield 1975) and personal observations. Each species was categorized by its biogeographic affinity by examining the current latitudinal boundaries of the species range relative to Monterey, California (Latitude: 36.59056°N). Species geographic ranges were gathered from previously published sources (Donat and Winfield 1975; Sagarin et al. 1999; Watanabe 2012). Northern species (N) were identified and those with ranges that occurred from Central California to Alaska, Southern species (S) have ranges that are within or extend from Central California to Baja California, and Cosmopolitan species (C) have ranges extending both north and south of Central California (or those with central CA as the core of their range). Species with a cosmopolitan (C) and southern (S) range are expected to have a higher presence on the experimental plates with elevated temperature due to their ability to thrive in warmer ocean temperatures. Based on previously noted studies in the Western Atlantic and Indian Ocean (Stachowicz *et al.* 2002; Smale *et al.* 2012;), cosmopolitan tunicates and bryozoans are expected to dominate the experimental plates due to their observed success as an invader.

2.3 Settlement Plate Array Design

Settlement plates for the heating experiments were 15 cm x 15 cm in size and constructed out of stainless steel to promote an even distribution of heat. Because the stainless steel was presumed to be a poor substrate for recruitment, the plates were

covered with inert nylon fabric to act as a settling surface. A similar nylon fabric was used in the study conducted by Smale and Wernberg (2012), which provides for an opportunity to compare results between studies.

The surfaces of the experimental plates were heated using 180 Watt silicon-rubber heat sheets (McMaster Carr) adhered to the back of the settling plate. In preliminary tests, experimental plates held a temperature increase of 2˚C over the ambient temperature at any given time. During the testing phase, thermal sensors measured significant increases in water temperature up to 4 mm from the plate surface. Temperatures were recorded by placing temperature probes at increasing distance from the submerged plate. For the experiment, eight control and eight experimental settling plates were fixed to a 2-dimensional PVC scaffolding consisting of four rows and four columns. Control and heated plates were aligned in a checkerboard fashion to negate any bias if an edge effect were to occur (Fig. 2). The scaffold was then suspended horizontally underwater beneath the dock, with settling surfaces facing the seafloor.

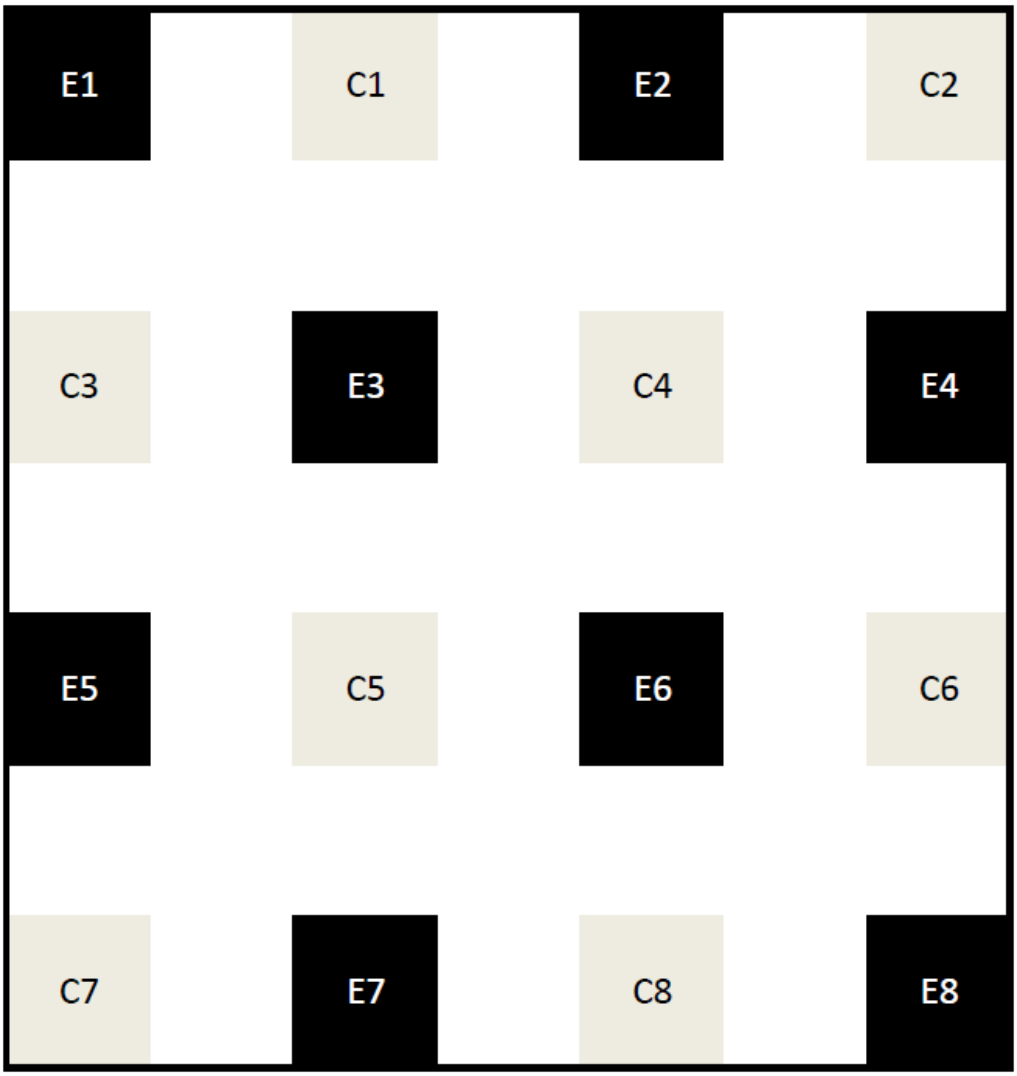

Figure 2. Spatial configuration of Experimental (E) and Control (C) settlement plates. Note: Experimental plate 6 (E6) experienced a malfunction and became a control plate, due to loss of heating capability.

A protective box, installed on the dock above the submerged plates, housed a hard drive and microprocessors that were connected to the settling plates by an underwater cable. A thermal sensor on the control plates read the ambient seawater temperature, relayed it to the dockside microprocessors, which controlled the heating elements to maintain a 2^{o} C elevated temperature on plate surfaces. This configuration allowed for raised temperatures on top of daily and seasonal fluctuations, as well as

shorter term variability. The software BASIC Stamp Editor v2.5.3 was used to program the microprocessors to perform heater control functions. The hard drive saved temperature readings on every control and heated plate every three seconds. However, automatic temperature data logging failed after one month and subsequent data logging was done once every week by manually connecting to the land-based control unit with a laptop computer running the software BASIC Stamp Editor v2.5.3 to monitor live temperature readings. This change in procedure did not affect the temperature regulation of the array.

2.4 Experimental Design

The experimental design consisted of a single treatment with a sustained temperature increase of 2°C over the ambient control group. The +2°C treatment level was selected based on the projected increases in Eastern Pacific global mean sea temperature within this century, which fall within the range of 1.5 – 3.5°C (IPCC 2014).

Settling plates were installed in the Monterey Harbor in May 2014 (Fig. 3), to capture the summer recruitment season, and were submerged for 129 days. Plates were photographed every two weeks to track community development. The array was checked biweekly to ensure that all components were in place and the hardware was functioning properly.

The hardware originally consisted of eight experimental and eight control settlement plates, however, due to failure in the heating capabilities of one experimental plate, the final design consisted of nine unheated control plates and seven heated experimental plates.

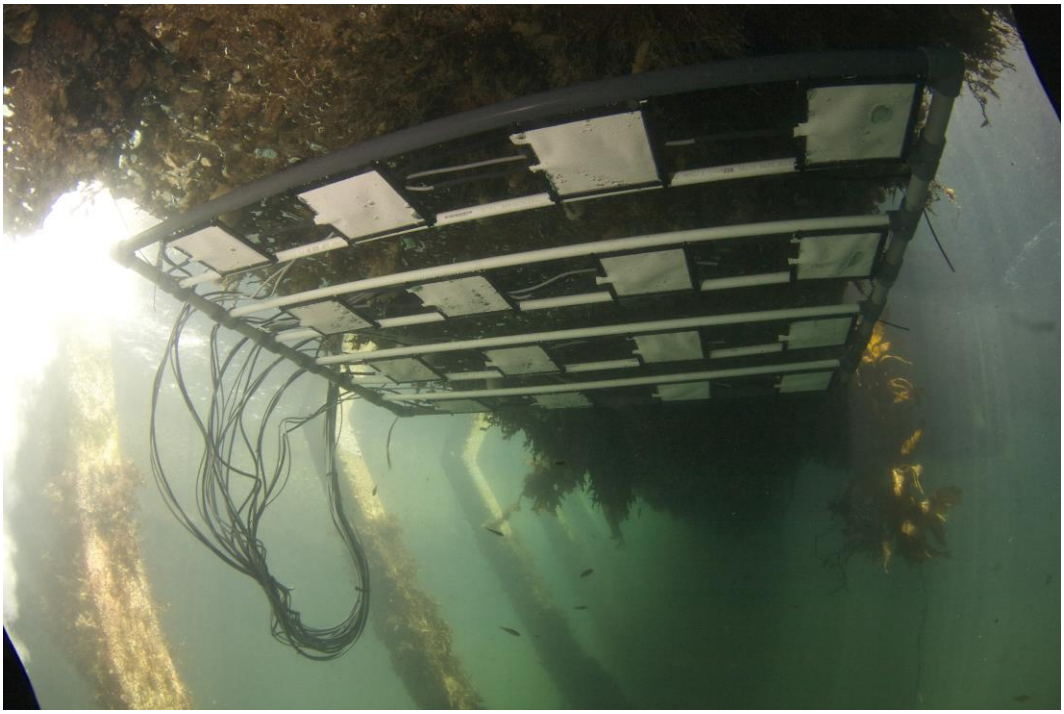

Figure 3. Installed array consisting of 16 settling plates mounted and hanging underneath floating dock of Monterey Harbor.

Once all plates had at least 50% cover of organisms, final pictures were taken and the plates were removed. Wet weight was obtained using a microbalance and rounded to a tenth of a gram to measure the change in biomass from the beginning to the end of the experiment.

2.5 Image Analysis

Photographs were used to track changes in species abundance and composition on each plate. Photos were taken with a Cannon DSLR camera with a 100mm lens. Plates were removed from the array for dockside photography and quickly returned. Photo sessions lasted 5 – 10 minutes.

Image analysis was conducted on pictures taken after 36, 50, 82, 115 and 129 days. Percent cover was quantified using the program PhotoQuad (Tyrgonis and Sini,

2012) to generate 100 random points on each photo. Organisms underneath each point were visually identified to species or lowest functional group using the *Light and Smith Manual* (Carlton et al., 2007) and assigned to the categories of native/invader and by biogeographic affinity (Table 1). New recruits were manually counted to quantify abundance and verified by checking their presence/absence on pictures taken at a previous time point.

2.6 Statistical Analysis

Multidimensional scaling (MDS) ordination was used to visualize the differences in community composition between the experimental and control plates throughout the 129 day period in the field. A square root transformation was performed on the raw species data prior to analysis. In the MDS ordination, species composition and abundance were reduced to a single point in multidimensional space and plotted in two dimensions such that similarity between plates were measured by Euclidian distances. PERMANOVA was used to test the significance of differences of multi-species community composition on the plates across my treatments using the program PRIMER 6 (PRIMER-E Ltd.). A similarity-percentages (SIMPER) test was used to identify the species that contribute most to the differences in community composition.

Repeated-measures ANOVAs (RM-ANOVA) were used to analyze percent cover trajectories through time. In cases where the assumption of sphericity was not met, I used Greenhouse-Geisser (G-G) adjustments of degrees of freedom according to the recommendation of Von Ende (1993). RM-ANOVAs were therefore used to look at changes in percent cover of taxa categorized into groups of native or invasive, and southern or northern biogeographic affinity between the control and heated plates. A

RM- ANOVA was also used to evaluate if the experimental group had differing recruitment rates compared to the control group.

To test whether experimental warming affected the response of sessile invertebrates based on each species biogeographic affinity, a two-way ANOVA was used to compare average final percent cover of Northern/Cold-Water and Southern/Warm-Water species; using biogeographic affinity and warming treatment group as the two factors. Cosmopolitan species were removed from biogeographic statistical analyses. To evaluate if invasive species occupy more space on the heated treatment plates than native species throughout the experiment, I conducted a two-way ANOVA with warming treatment and native vs invasive identity as the two factors.

A two sample *t*-test was also used to compare the final average wet weight between the treatment groups. Diversity was measured for each plate on each date using Shannon-Wiener Diversity Indices, where p_i represents the proportional abundance of the *i*th species. Diversity was then measured throughout time between the control and heated treatment groups using RM-ANOVA.

$$H = -\sum_{i=1}^{k} p_i * \ln(p_i)$$

3.0 Results

Plates remained in the harbor for 129 days where the temperature difference between control and heated plates remained constant on top of natural fluctuations in ocean temperatures (Fig. 4). Mean thermal separation between control and experimental groups was 2.54 ± 0.65°C.

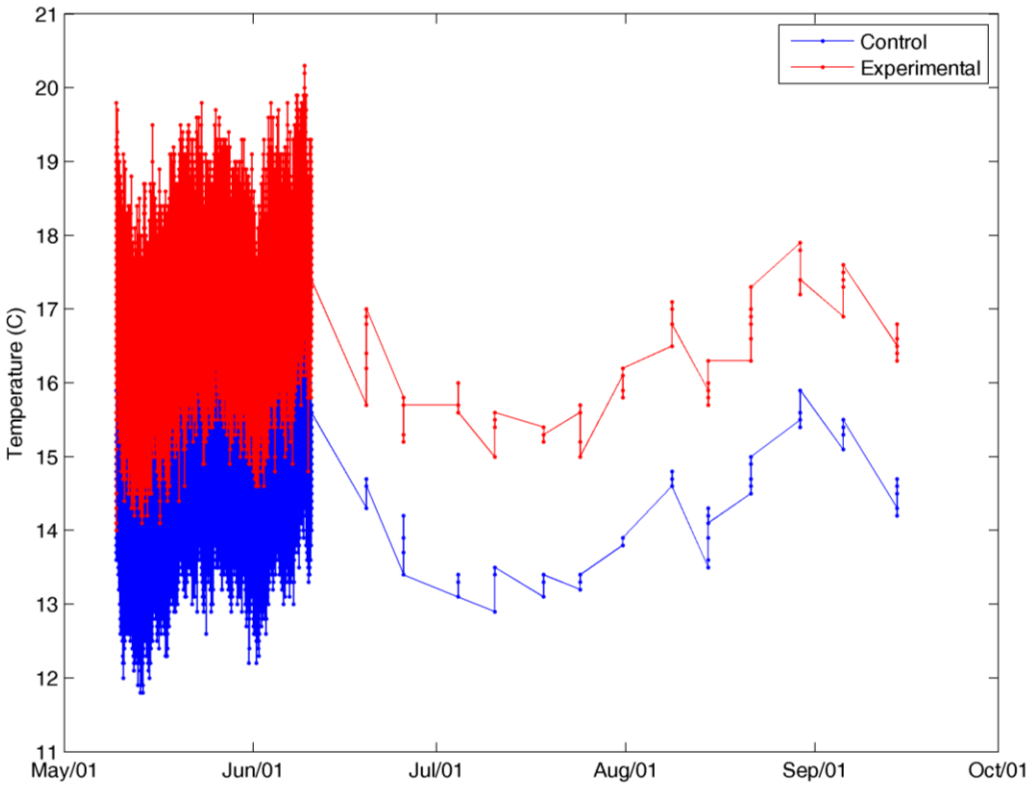

Figure 4. Data log from thermal sensors on Control and Heated plates. Recordings show a clear elevated temperature on the Experimental plates consistently held throughout the duration of the experiment. Lower frequency temperature logging occurred after the first month due to loss of automatic 3 second data logging capability.

There were twelve species that recruited and grew on the settlement plates and all but one species were found on both the control and heated plates (Table 1). 55% of these species were non-native. The plates were mostly dominated by colonial bryozoans and tunicates (Fig. 5). An unidentified sponge in the genus *Halichondria* was only found on the heated plates. Average percent cover of all species over time show differing rates of cover between the control and heated treatment groups (Fig. 6).

Average percent cover of species on control and heated treatments plates after 129 days show significantly more bare space on control groups (t_{10} = -7.31, p = 0.0001) (Fig. 7).

Table 1. *Species present across treatments.*
Biogeographic Affinity: C, Cosmopolitan; N, Northern; S, Southern; I, Introduced.

Species Name	Group Name	Biogeographic Affinity	Native Range
Spirorbinae	Annelida	C	Worldwide
Serpula columbiana	Annelida	N	Alaska - Southern California
Tube-Building Annelid	Annelida	-	-
Celleporaria brunnea	Bryozoa	S	Oregon - Ecuador
Watersipora subtorquata	Bryozoa	C/I	Worldwide
Bugula neritina	Bryozoa	S/I	Central Ca - Baja, California Mexico
Bowerbankia sp.	Bryozoa	C/I	Puget Sound to Gulf of California
Botryllus schlosseri	Ascidiacea	C/I	Worldwide
Botrylloides violaceus	Ascidiacea	N/I	NW Pacific - Northern China
Ciona spp.	Ascidiacea	N/I	Alaska - Southern California
Ascidia ceratodes	Ascidiacea	C	British Colombia - Costa Rica
Halichondria sp.	Porifera	C	Worldwide

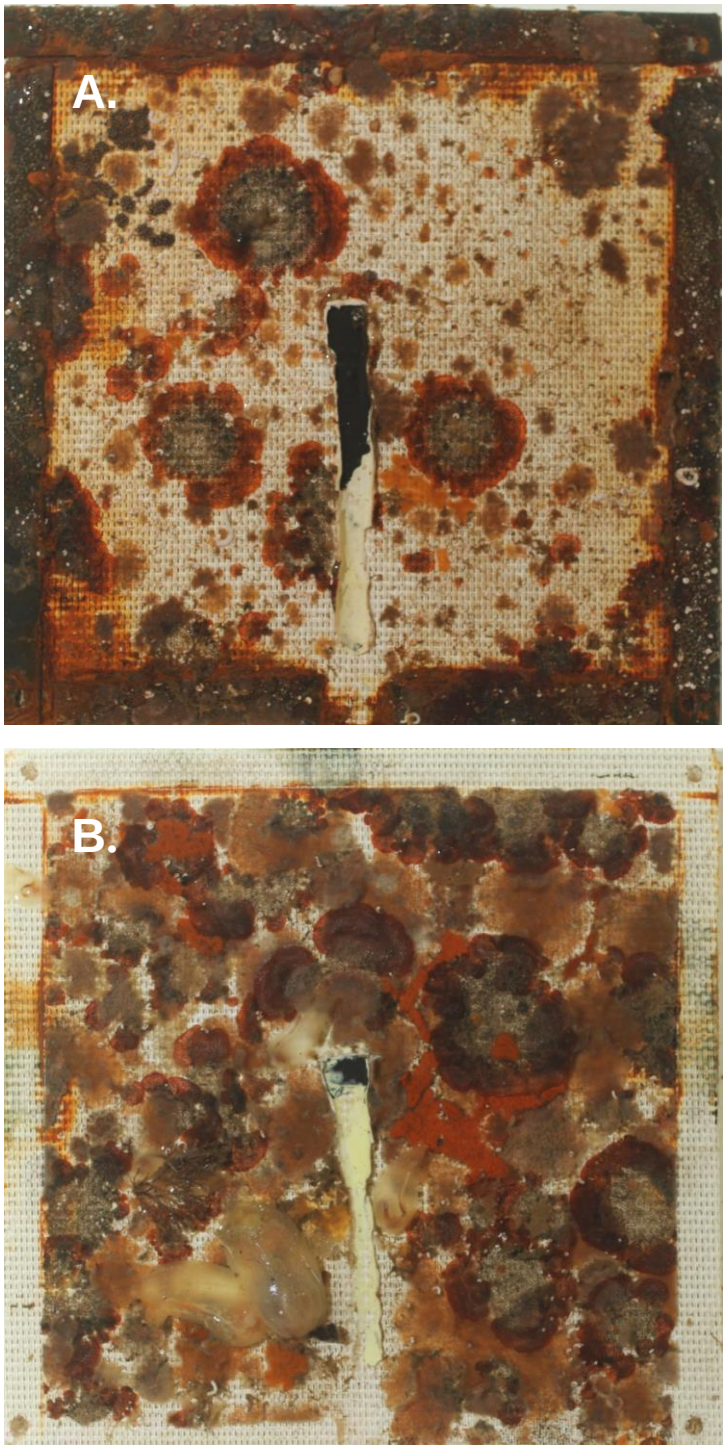

Figure 5. Photos depicting sessile community composition on a typical control (A) and heated (B) plate after 129 days of deployment in Monterey Harbor, CA.

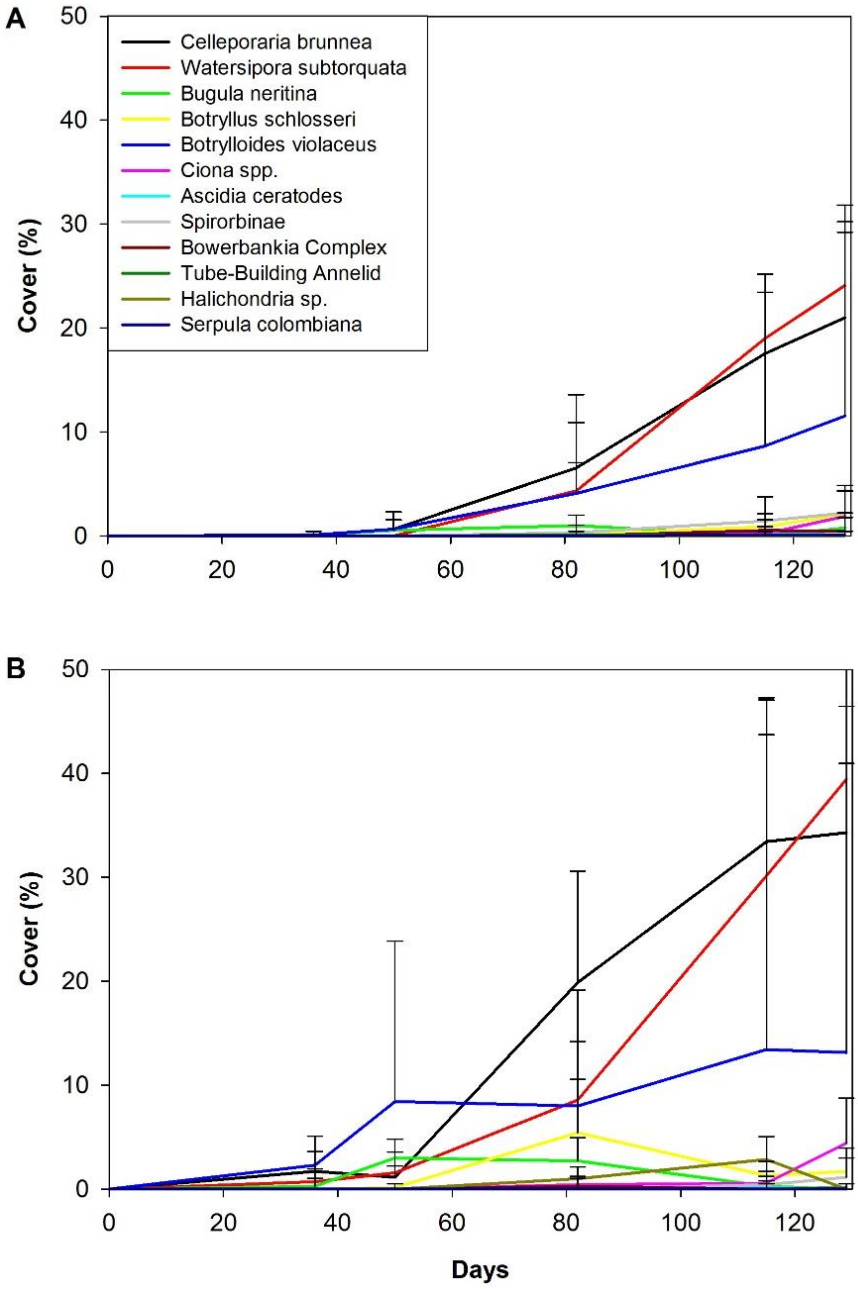

Figure 6. Time series showing average species percent cover (+S.E.) on control (A) and heated plates (B) over the duration of the experiment. Species are seen arriving and colonizing at different rate between the control and experimental plates.

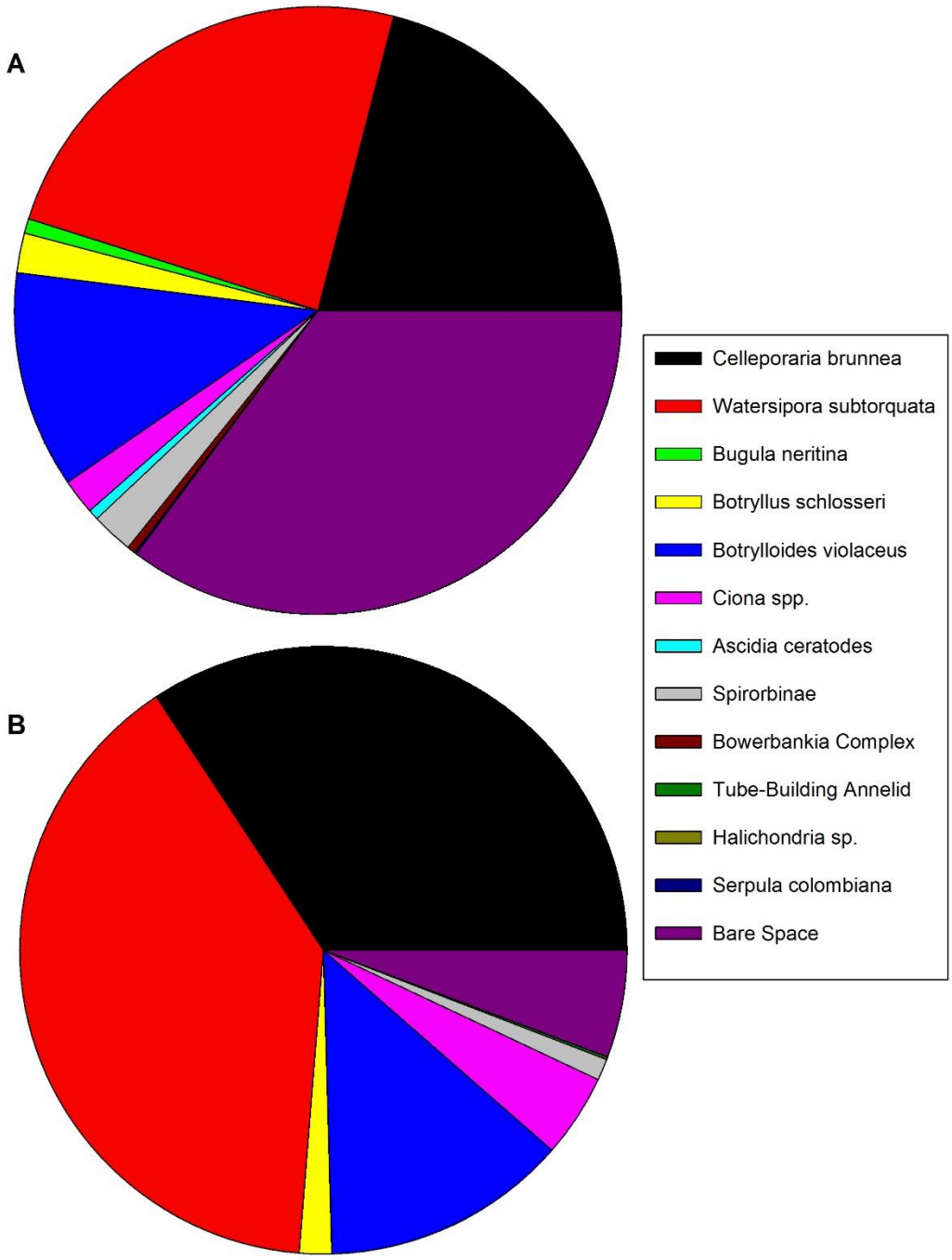

Figure 7. Percent cover of species after 129 days on control (A) and heated (B) treatment groups. The heated treatment group has significantly more cover of living organisms than control group. The species *W. subtorquata*, *C. brunnea* and *B. violaceus* contribute to the most cover on both types of settlement plates.

The heated experimental group exhibited a significantly higher rate of recruitment up until day 80 of the experiment (RM-ANOVA, Treatment*Time, $F_{1,14} = 3.56$, $p < 0.001$). A significant time factor indicates an increase of recruitment over time while the time*treatment factor shows differing trajectories between control and heated groups over time (Table 2). As settlement and growth increased and available bare space declined, there was a tapering and decrease in recruitment on both the control and heated treatment groups (Fig. 8A). When looking at average cumulative recruitment over time (Fig. 8B), there is also a significantly different trajectory between the control and heated treatment groups (Table 2), but their total recruitment at the end of the study was similar.

Table 2. *Summary of statistics for RM-ANOVA comparing new (A) and cumulative (B) recruitment throughout the experiment. G-G modification was used for the factors Time and Time*Treatment.*

(A) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	0.6637	1, 14	0.4289
Time	62.9695	2.2089, 30.925	<.0001*
Time* Treatment	20.6	2.2089, 30.925	<.0001*

(B) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	7.379	1, 14	0.0167
Time	447.285	1.6611, 23.255	<.0001*
Time* Treatment	10.1462	1.6611, 23.255	0.0012

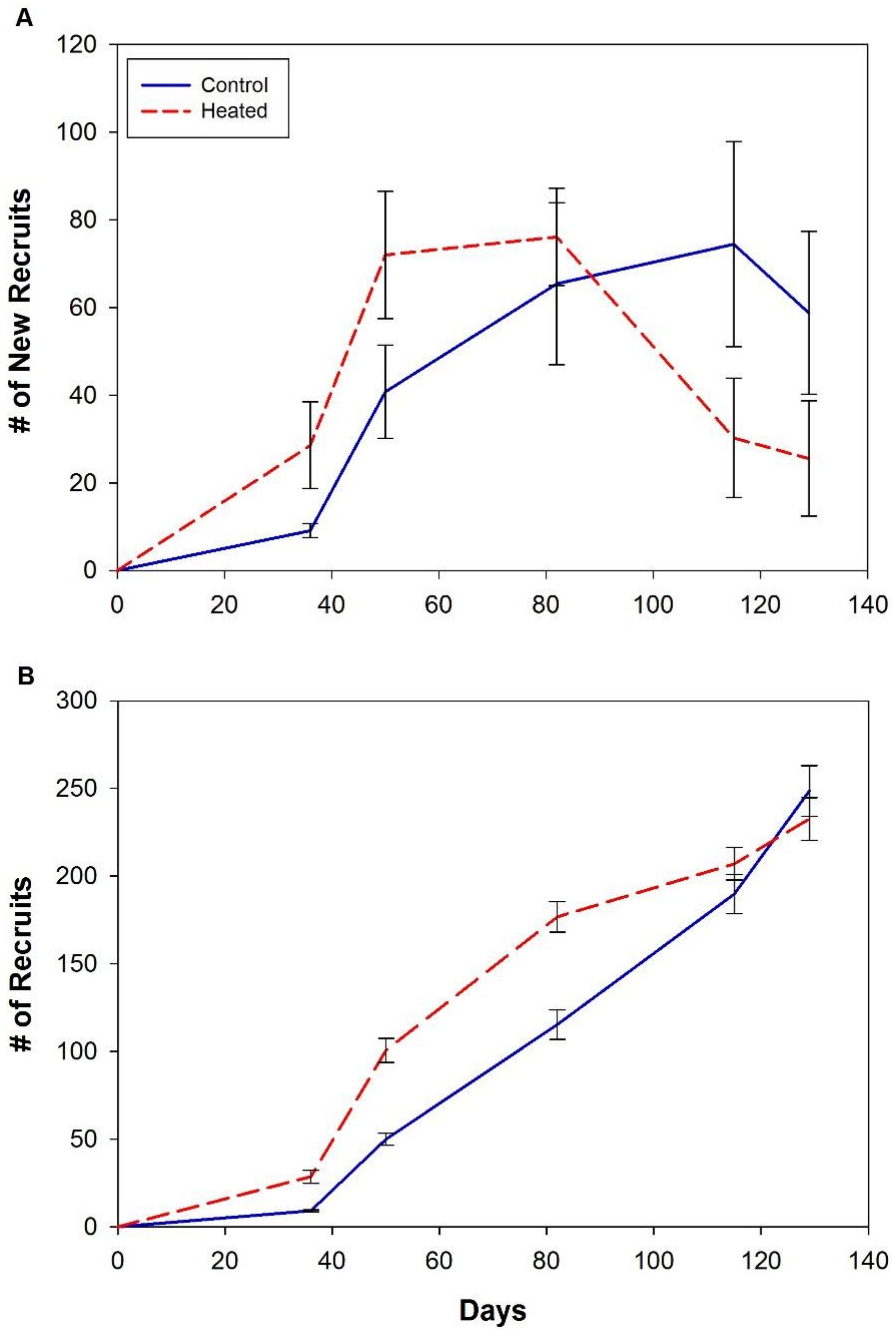

Figure 8. (A) Trajectories and mean # of new recruits between the heated and control groups are significantly different. Early and higher rates of recruitment were seen in the experimental group. (B) Average cumulative number of recruits over time between control and heated treatment show significantly different trajectories, but similar total recruitment after 129 days. Values represent the mean for each treatment ± 1 SE.

To test for differences in percent cover between the control and heated treatments over the course of the experiment, RM-ANOVA were conducted across the four time points (Fig. 9) showing the experimental group had significantly more cover across all time points (Table 3). In addition, the heated treatment group weighed (g) on average 33% more than the control group after at 129 days (t_{10} = 3.39, p = 0.0067) (Fig. 10). Average increase in percent cover per day for the control group was 0.20 g, while the heated treatment was 0.30 g per day.

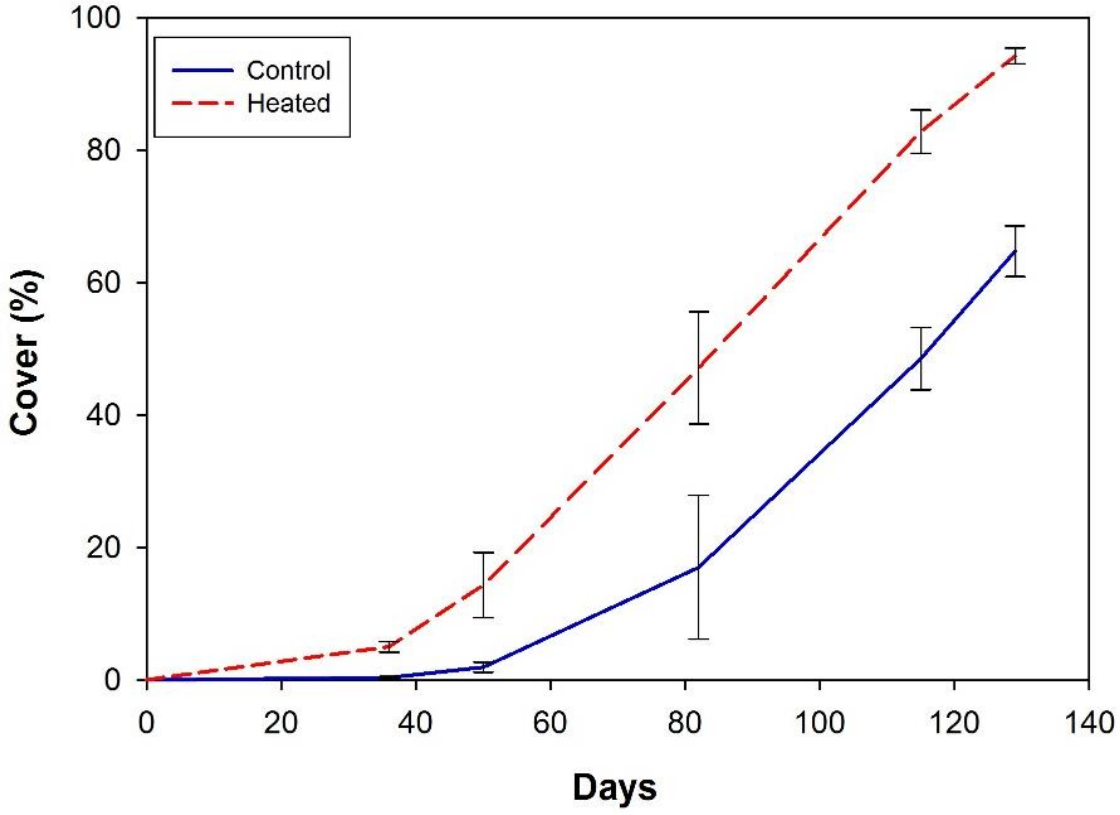

Figure 9. Average percent cover (± 1 SE) over time shows a clear and significant increase in fouling by the heated experimental group throughout the study.

Table 3. *Summary of statistics for RM-ANOVA comparing average percent cover on the control and experimental groups. G-G modification was used for the factors Time and Time*Treatment.*

Factor	Exact F	NumDF, DenDF	P-Value
Treatment	52.9617	1, 14	<.0001*
Time	332.8643	2.6621, 37.27	<.0001*
Time* Treatment	11.8755	2.6621, 37.27	<.0001*

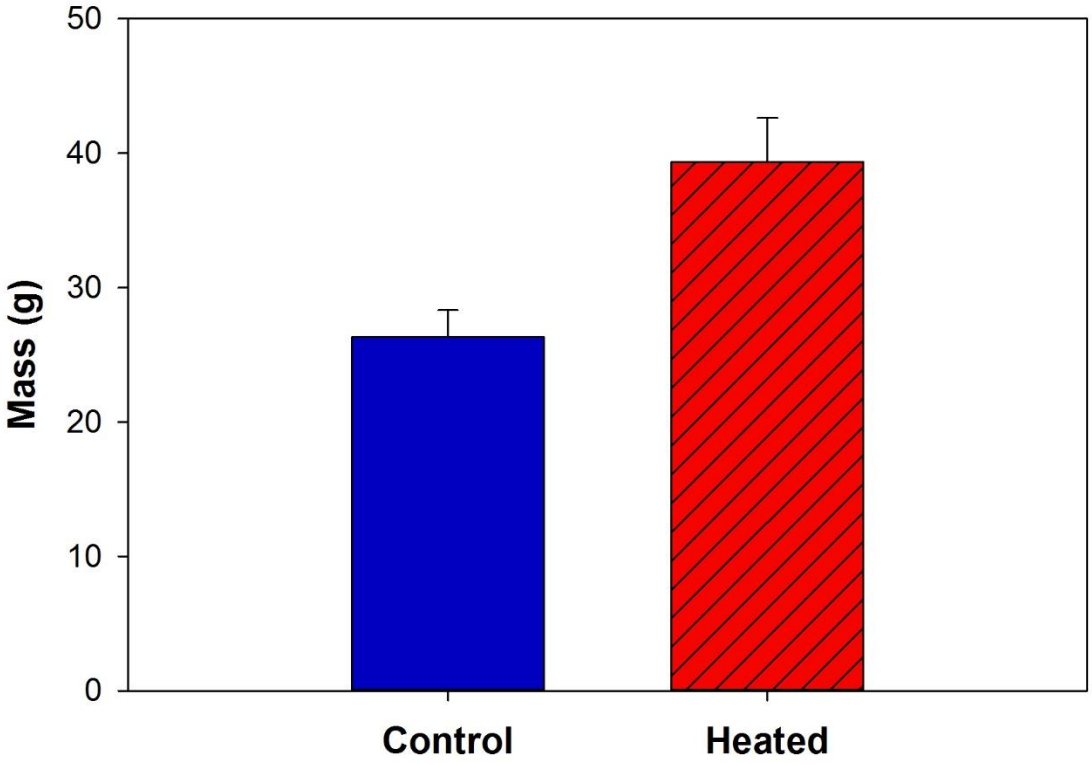

Figure 10. Comparison of average wet weight (g) (± 1 SE) of organisms on settlement tiles (tile weight subtracted) in the control and experimental warming treatments after 129 days in the field.

Shannon-Wiener Diversity indexes were calculated to quantify differences in biodiversity between the heated and control treatments throughout the 129 day duration of tile deployment. Because the heated plates saw greater average recruitment earlier than the control plates, the experimental plates were more diverse on earlier sampling dates (Fig. 11, Table 11). However after day 82, the control plates achieved and maintained a similar diversity score to the heated plates for the remainder of the experiment.

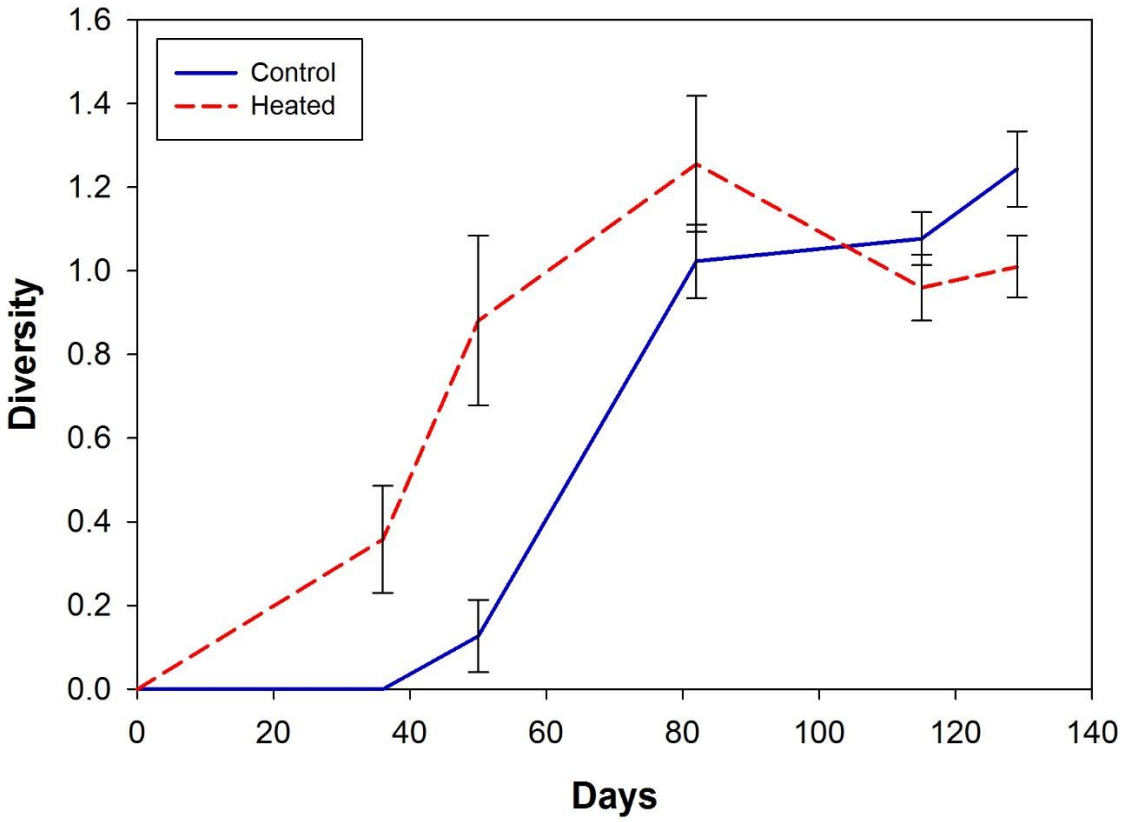

Figure 11. Trajectory of mean diversity (±S.E.) shows there was not significant differences in the control and experimental groups over time. Early recruitment on the experimental plates contributed to an earlier increse in diversity however, by day 80 the diversity in both groups was about the same since the majority of species found were present in both control and experimental groups.

Table 4: *Summary of statistics for RM-ANOVA comparing diversity between control and experimental groups. G-G modification was used for the factors Time and Time*Treatment.*

Factor	Exact F	NumDF, DenDF	P-Value
Treatment	4.0076	1, 14	0.0651
Time	69.4712	2.4964, 34.949	<.0001*
Time* Treatment	10.7126	2.4964, 34.949	<.0001*

Species varied in relative abundance over time, but assemblages remained distinct between the control and heated treatments. There was an increase in the presence of uncolonized space on the control plates, which was revealed by a SIMPER test and contributed to 34% of the difference when compared to the heated treatment group in the final time point (Fig. 12, Table 5 and 6). *Botrylloides violaceus* (32%), *Watersipora subtorquata* (19%) and *Celleporaria brunnea* (13%) accounted for the rest of the difference. When bare space was removed from the MDS ordinations, *B. violaceus*, *W. subtorquata* and *C .brunnea* were again the major contributors of difference, accounting for ~98% of the difference between the assemblages of the control and experimental group (Fig. 13, Table 8). Similarly, PERMANOVA tests (Table 7) reported significant differences between treatments in all time points except for at 115 days when bare space was removed. An MDS plot of species composition averaged over all plates in each treatment at each time point (Fig. 14, Table 9) is a useful visualization because it tracks the two groups through time. The resulting graph shows the divergence of developmental pathways for each group caused by differing recruitment rates and community composition of species listed above.

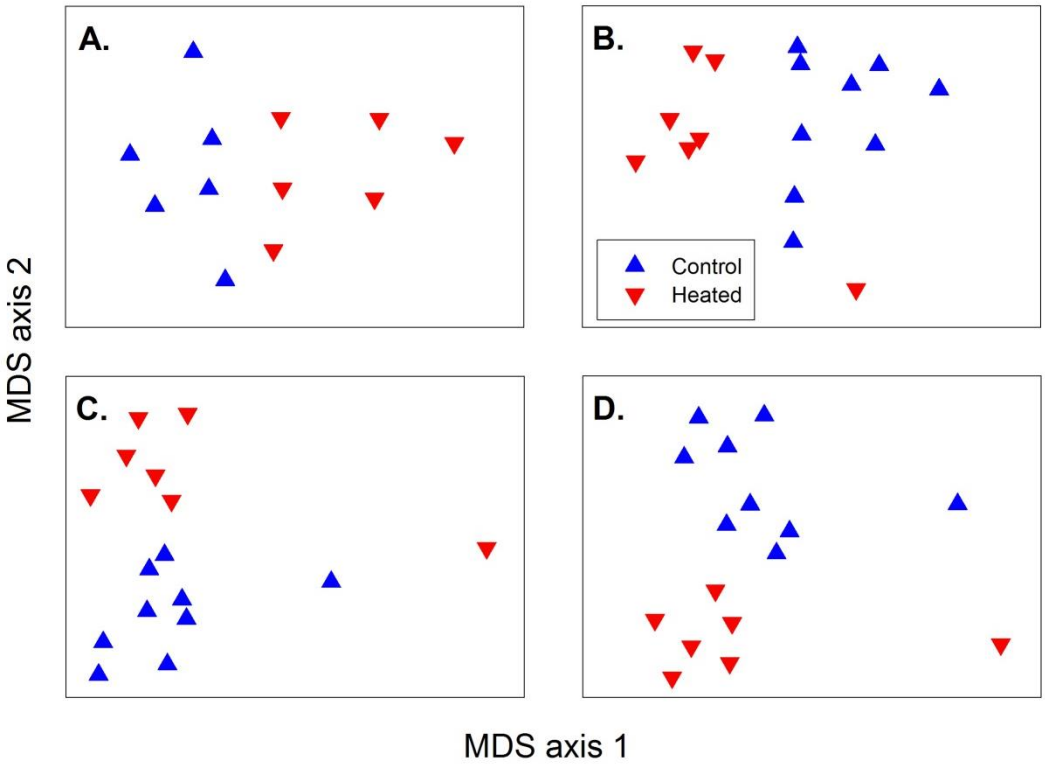

Figure 12. nMDS plots representing species composition on control and heated treatment groups across time, including bare space, in the test at 50 (a), 82 (b), 115 (c), and 129 (d) days. Labels on points refer to individual plates.

Table 5. *Summary of statistics for a PERMANOVA test corresponding to the MDS ordinations (Fig. 5) show the plate composition on the control and heated treatment groups were significantly different on each time point.*

Time (Days)	Source	DF	SS	MS	P (Perm)
50	Treatment	1	23.596	23.596	0.001
	Resemblance	14	56.513	4.0366	
	Total	15	80.109		
82	Treatment	1	55.529	52.529	0.003
	Resemblance	14	131.19	9.3705	
	Total	15	183.71		
115	Treatment	1	63.053	63.053	0.001
	Resemblance	14	186.97	13.355	
	Total	15	250.02		
129	Treatment	1	68.837	68.837	0.001
	Resemblance	14	192.12	13.723	
	Total	15	260.96		

Table 6. *Summary of statistics for a SIMPER Test corresponding to the MDS ordinations (Fig. 5) show 98.16% of the differences between the control and heated treatment group were due to differing percent cover of Bare Space, Botrylloides violaceus, Watersipora subtorquata and Celleporaria brunnea.*

Variable	Control Av.Value	Experimental Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Bare Space	35.2	5.71	998	1.42	34	34
Botrylloides violaceus	11.6	13.1	943	0.53	32.12	66.12
Watersipora subtorquata	24.1	39.4	561	0.86	19.11	85.23
Celleporaria brunnea	21	34.3	380	0.91	12.93	98.16

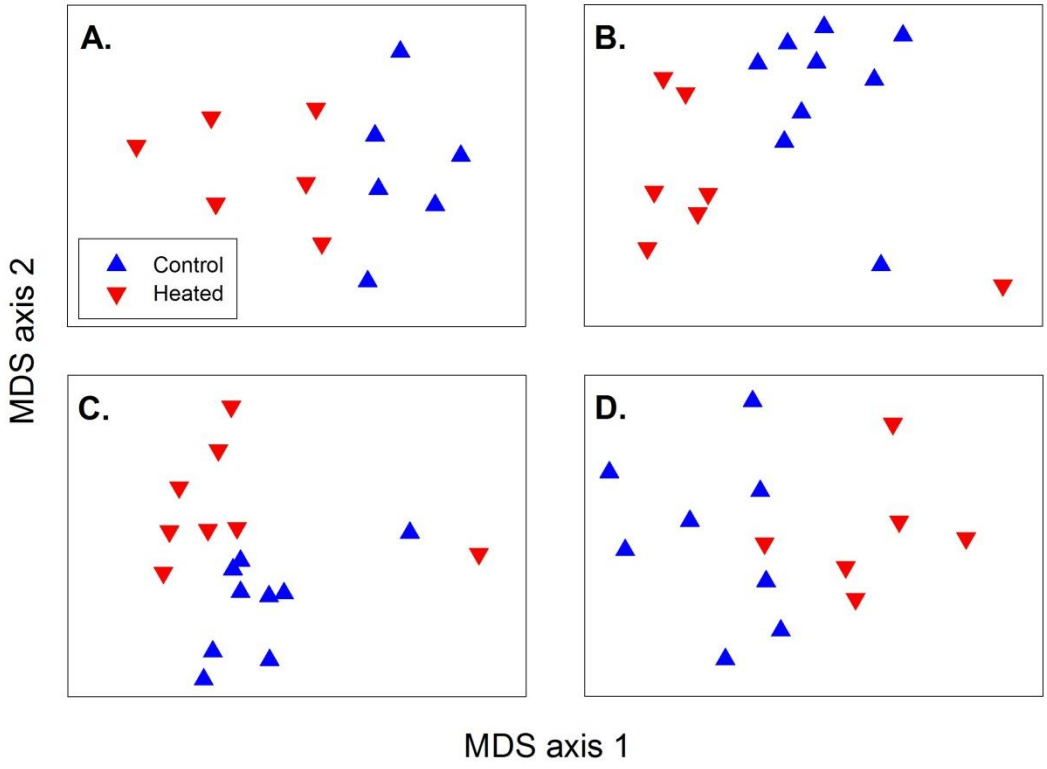

Figure 13. nMDS plots representing species composition on control and heated treatment groups across time, sans bare space, in the test at 50 (a), 82 (b), 115 (c), and 129 (d) days. Labels on points refer to individual plates.

Table 7. *Summary of statistics for a PERMANOVA test corresponding to the MDS ordinations (Fig.6) show the plate composition on the control and heated treatment groups were significantly different on each time point.*

Time (Days)	Source	DF	SS	MS	P (Perm)
50	Treatment	1	23.596	23.596	0.001
	Resemblance	14	56.513	4.0366	
	Total	15	80.109		
85	Treatment	1	39.141	39.141	0.007
	Resemblance	14	125.87	8.9909	
	Total	15	165.01		
115	Treatment	1	23.363	23.363	0.125
	Resemblance	14	166.7	11.907	
	Total	15	190.06		
129	Treatment	1	22.456	22.456	0.001
	Resemblance	14	78.92	6.5767	
	Total	15	101.38		

Table 8. *Summary of statistics for a SIMPER test corresponding to the MDS ordinations (Fig. 6) show 98.16% of the differences between the control and heated treatment group were due to differing percent cover of the three species B. violaceus, W. subtorquata and C. brunnea.*

Variable	Control Av.Value	Experimental Av.Value	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Botrylloides violaceus	11.6	13.1	943	0.53	48.67	48.67
Watersipora subtorquata	24.1	39.4	561	0.86	28.95	77.62
Celleporaria brunnea	21	34.3	380	0.91	19.59	97.21

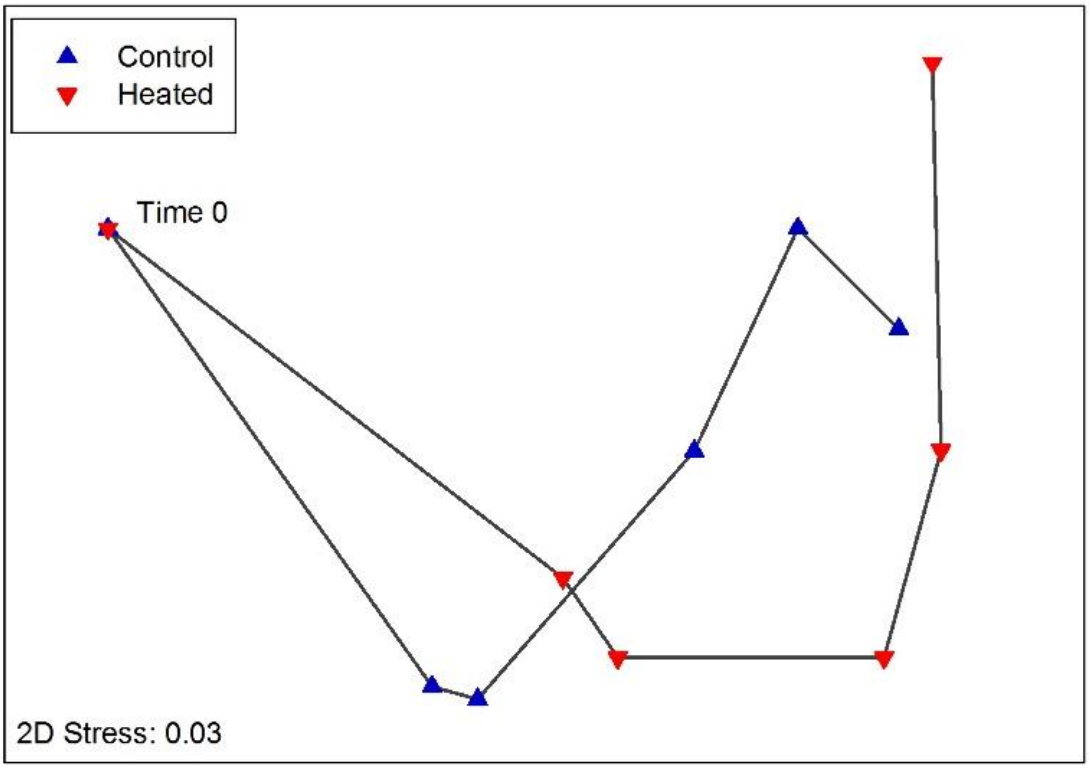

Figure 14. Divergence of average community development after 129 days. Early recruitment and greater overall percent cover of organisms on the heated plates contributed to the diverging community trajectories.

Table 9. *Summary of statistics for average temporal MDS Ordination.*

Source	df	SS	MS	Pseudo-F	P(perm)
Day	5	50.173	10.035	9.1722	0.003
Treatment	1	2.8266	2.8266	2.5837	0.051
Resemblance	5	5.4701	1.094		
Total	11	58.47			

Southern and Northern species were also tracked over time (Fig. 15) and both biogeographic groups increased in percent cover over time. The Southern/Warm-Water species showed a significant Treatment and Time*Treatment effect while the Northern/Cold-Water species did not (Table 10). There were significantly more Southern/Warm-Water species on both control and heated plates compared to

Northern/Cold-Water species. Northern/Cold-Water species increased in percent cover over time, however the increase in temperature on the heated plates did not induce any significant differences compared to the controls (Table 10). A two-way ANOVA showed neither native source region (north vs south) nor heating affected final cover (Table 11).

There was a significant increase of cover by both native and invasive species on the heated plates compared to the control plates (Table 12, Fig. 17). There is only a time*treatment effect for invasive species, indicating that the trajectories diverged significantly over time (Table 12). A two-way ANOVA showed that there was a significant treatment effect on both native and invasive species, however the composition did not change between the control and heated groups (Table 13).

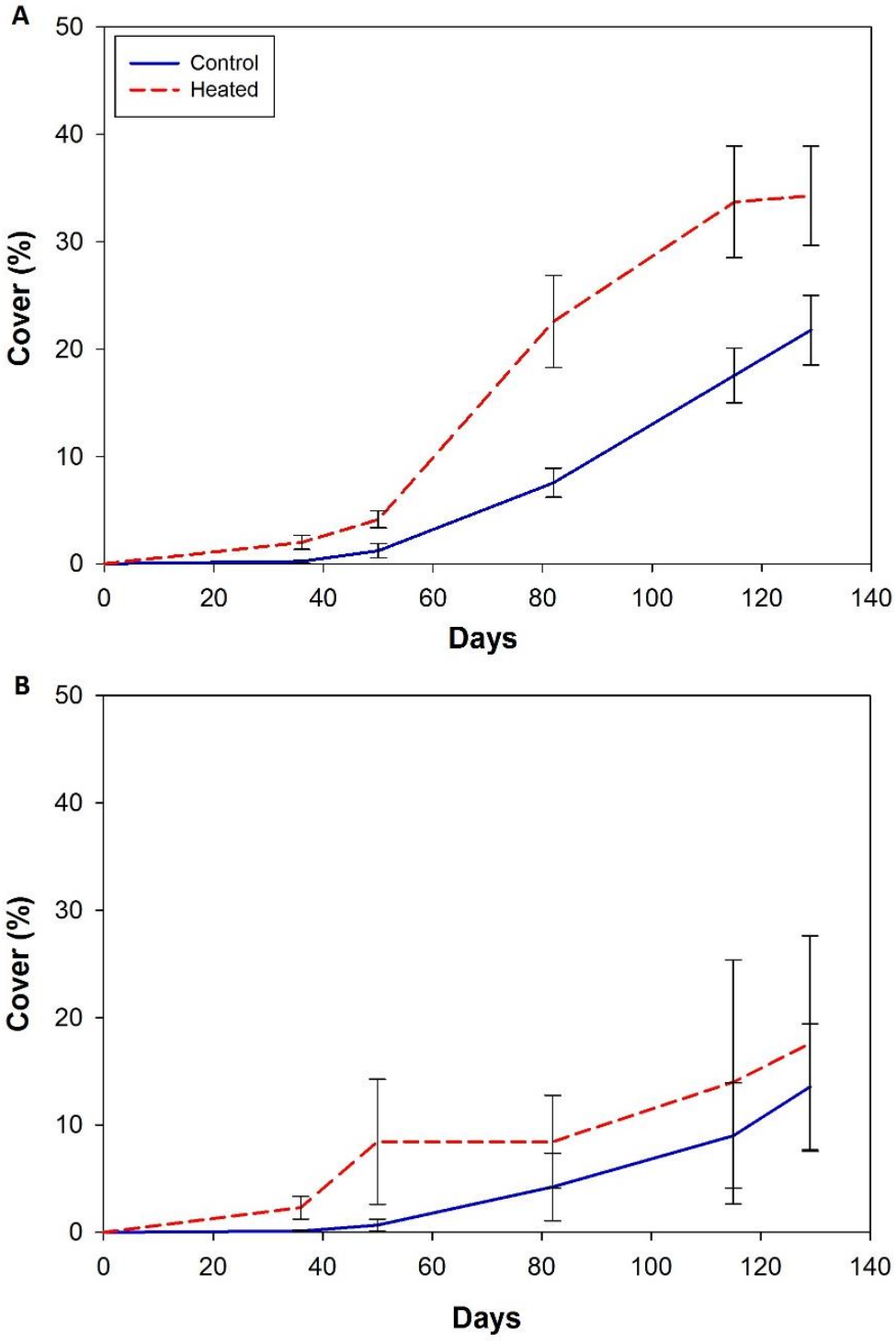

Figure 15. Average percent cover (± 1 SE) of Southern/Warm-Water Species (A) and Northern/Cold-Water Species (B) over time between the experimental warming treatment groups indicate that the heated plates promoted a significant increase of southern/ warm-water species compared to the ambient control plates.

Table 10. *Summary of Statistics for Repeated Measures ANOVA: Average Southern/ Warm-Water (A) and Northern/ Cold-Water (B) Species Development over time between treatment groups. G-G modification was used for the factors Time and Time*Treatment.*

(A) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	11.1974	1, 14	0.0048*
Time	70.9011	1.8344, 25.681	<.0001*
Time* Treatment	5.2802	1.8344, 25.681	0.0138

(B) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	0.51	1, 14	0.4869
Time	5.4617	1.3002, 18.203	0.0238*
Time* Treatment	0.1732	1.3002, 18.203	0.7468

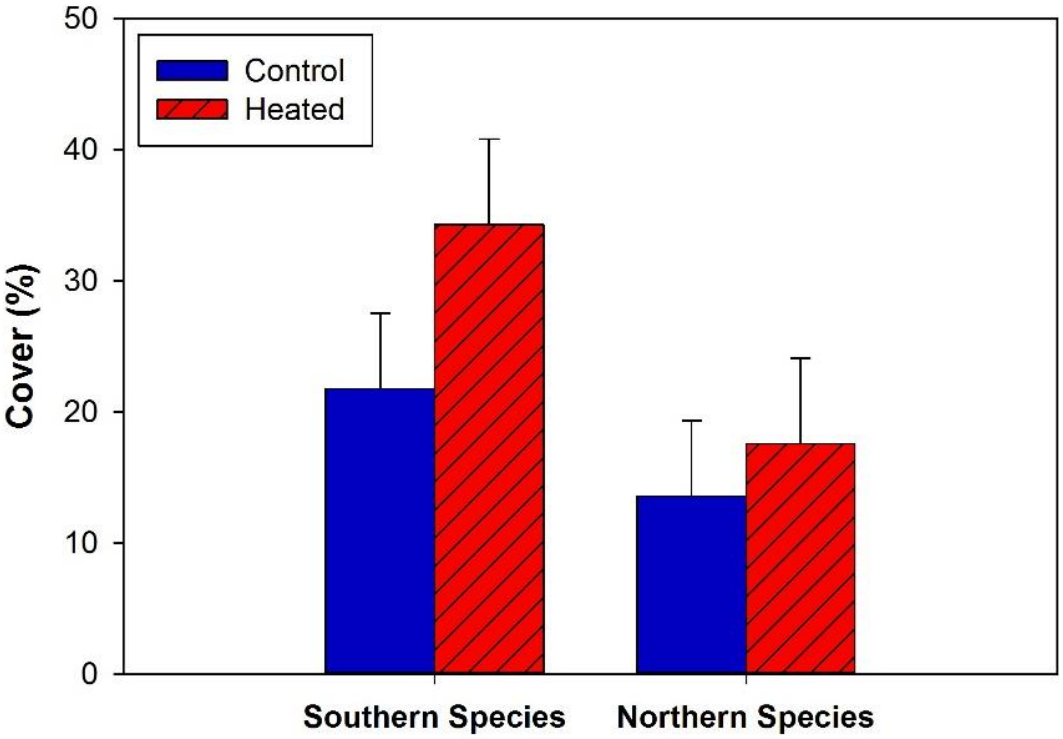

Figure 16. Final mean percent cover (±S.E.) of Southern/Warm-Water and Northern/Cold-Water species show the effects of warming induce a significant increase in percent cover in both groups.

Table 11. *Summary statistics for a Two-Way ANOVA comparing the final mean percent cover between two biogeographic regions*.

Effect Tests				
Source	DF	Sum of Squares	F Ratio	P-Value
Biogeographic Affinity	1	1224.227	4.0979	0.0526
Treatment	1	537.5402	1.7993	0.1906
Biogeographic Affinity*Treatment	1	141.9767	0.4752	0.4963

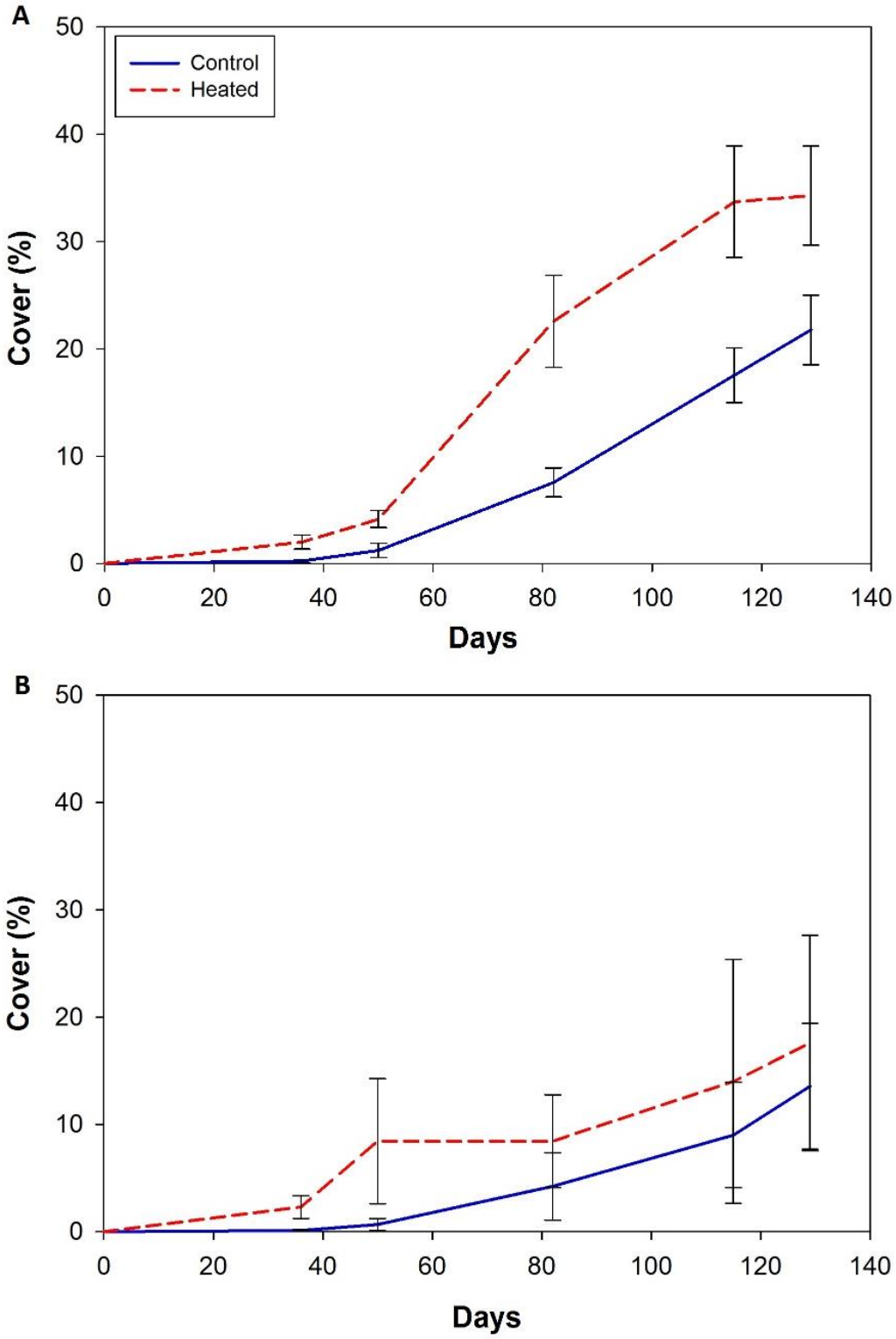

Figure 17. Average percent cover (± 1SE) of native (A) and invasive (B) species development over time between control and heated treatment groups.

Table 12. *Summary of statistics from RM-ANOVA comparing native (A) and invasive (B) species development over time between control and heated treatment groups. G-G modification was used for the factors Time and Time*Treatment.*

(A) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	6.6032	1, 14	0.0223*
Time	86.6504	1.733, 24.262	<.0001*
Time* Treatment	1.8559	1.733, 24.282	0.1813

(B) Factor	Exact F	NumDF, DenDF	P-Value
Treatment	9.4408	1, 14	0.0083*
Time	73.5228	1.862, 26.061	<.0001*
Time* Treatment	5.4231	1.8615, 26.061	0.0121

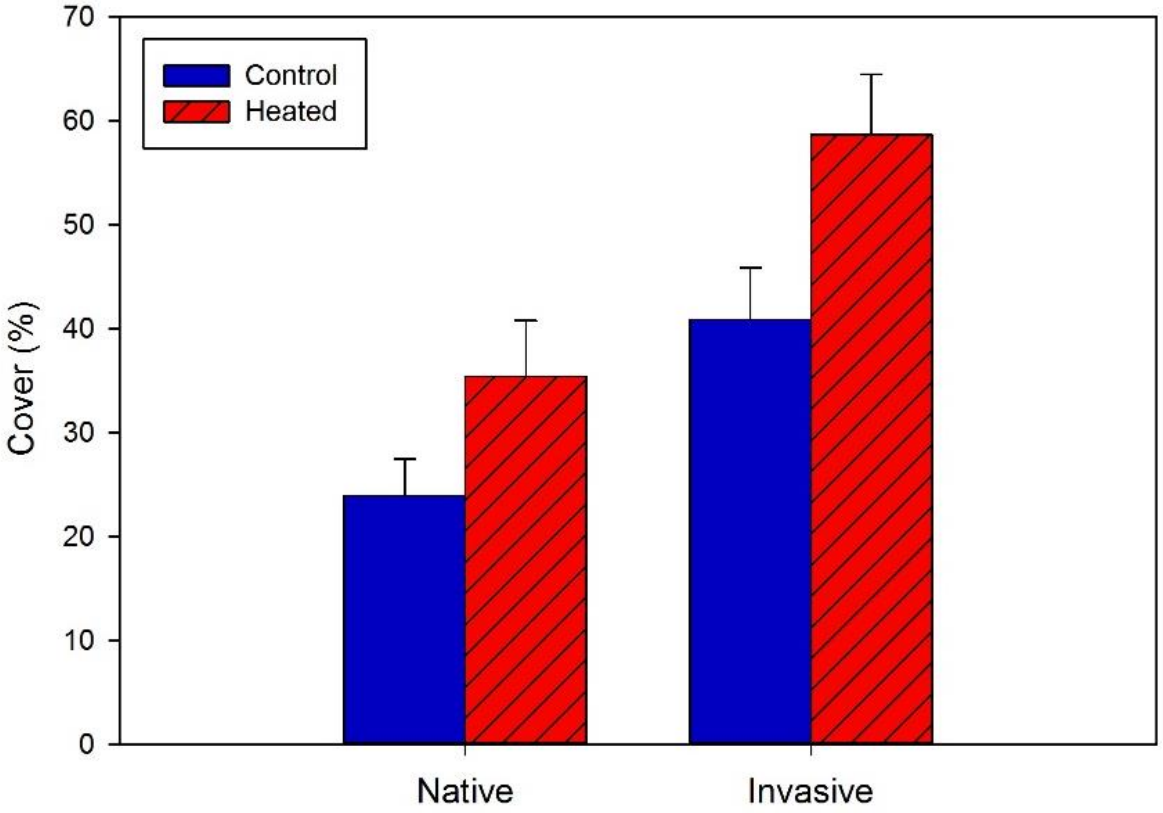

Figure 18. Final average percent cover (±S.E.) of native and invasive species across treatment groups after 128 days, show significantly more invasive and native species on the heated treatment plates.

Table 13. *Summary of statistics for 2-Way ANOVA comparing native and invasive species presence between the control and experimental plates.*

Effect Tests				
Source	DF	Sum of Squares	F Ratio	P-value
Treatment	1	1697.669	8.7526	0.0062*
Status	1	3195.161	16.4732	0.0004*
Treatment*Status	1	77.7857	0.401	0.5317

4.0 Discussion

The restructuring of sessile assemblages due to temperature fluctuations can have profound effects on extant ecosystems dynamics. By experimentally increasing the temperature of settling plates by 2.5°C, the local Monterey Harbor marine fouling community experienced shifts in species abundance and assemblage development. Normal ocean temperature ranges in Monterey typically fluctuate beyond 2.5°C; however, when this marginal increase in temperature is maintained, it can allow for significant changes in the community composition. The findings of this study support the hypotheses concerning community development and the increased abundance of southern/warm-water species and invasive species on the experimentally heated plates. The heated plates affected the trajectory of native northern and southern species accumulation, but not the final cover (Table 10 and 11). Invasive species were more prevalent in all treatments and were significantly enhanced on the heated plates.

Heated plates maintained greater percent coverage of living sessile taxa for each time point during the experiment (Fig. 9). Increased percent cover of colonial taxa on the plates contributed to the significant difference in overall biomass in the treatment group compared with the control group. The increase of percent cover in the heated treatment could be attributed to new recruits or faster growth from previously settled organisms. However, due to the significantly higher recruitment to the warm tiles in the early stages (Fig. 8) it is likely that the increase in percent cover is due to enhanced recruitment rates and faster growth upon settlement. The increased growth on heated plates could be attributed to higher metabolic rates associated with beneficial increases in temperature. The tapering off of recruitment rates in both control and heated

treatment groups is likely due to a decrease in available bare space to recruit on over time.

Further examination of percent cover by southern/warm-water species showed a significant earlier increase on the heated plates compared to the controls (Table 11). This is not surprising since the heated plates mimic a thermal environment closer to that of their native range. Surprisingly, northern/cold-water species also significantly increased in percent cover on the heated tiles over time as well (Table 11). According to Shelford's Law of Tolerance (Shelford 1931), which states that species have both an optimum and a tolerated range of living temperatures, it is likely that many of the species currently living in Monterey Harbor are living on the tail end of this spectrum. The increase in temperature is presumed to shift the southern/warm-water species away from their lower end of thermal tolerance and closer towards the peak of their "optimal zone," which allows for more efficient homeostatic functioning and therefore increased competitive ability and growth rates (Elliot 1976, Portner et al. 1998). Northern/cold-water species, however, would theoretically be stressed since they already inhabit the higher limits of their thermal range. Clearly, this is not the case and organisms with northern native ranges (*Serpula columbiana, Botrylloides violaceus* and *Ciona sp*.) appear to be suitably adapted to not only weather but flourish when ambient temperatures are increased ~2.5°C.

Invasive species also exhibited a significantly enhanced cover on the heated plates (Fig. 16). Invasive species that successfully invaded a new environment may have broad niche requirements and may be better adapted to variable and fluctuating environmental conditions. The invasive species could have either found the experimental plates simply more hospitable and closer to the temperatures of their

native range or they flourished under the experimental conditions because they have broader temperature tolerances. Successful invasive species are known to have a higher expression of Heat Shock Proteins (HSP), a mechanism by which some species can gain a competitive advantage when increases in temperature create stressful situations. Production of HSPs allows for greater thermal tolerance causing proper homeostatic functioning compared with organisms incapable of producing enough HSPs (Somero 2002, Tomanek & Sanford 2003, Zerebecki & Sorte 2011). Although high levels of HSPs are commonly linked with successful invaders when discussing climate change and biogeography, they do not seem to be influential in this experiment because native species, who may have the ability to express high levels of HSPs, also had a positive response to warming.

The MDS ordinations confirm there were significant compositional differences between the control and experimental plates throughout the experiment. The SIMPER analysis showed that 97.2% of the difference between the two treatments was caused by the increase of the calcifying bryozoans *Watersipora subtorquata*, *Celleporaria brunnea* and the colonial tunicate *Botrylloides violaceus* on the heated plates. The increase in abundance of *W. subtorquata* and *B. violaceus* is worrisome because both species are successful worldwide invaders (Lambert & Lambert 2003, Mackie *et al*. 2012) that cause fouling damage to harbors and vessels. The temporal MDS is useful to track the total average compositional trajectories of the heated and control groups. Early divergence between the control and heated treatment groups is due to the increased rate of recruitment on the heated tiles followed by differing proportions of *W. subtorquota*, *C. brunnea* and *B.violaceus*. The trajectories are not completely disparate, which is not surprising because all but one species were found on both treatments,

which is corroborated by the insignificant differences in the Shannon-Weiner values generated for both control and experimental groups (Fig. 11).

Comparing the data from this study to Smale and Wernberg's (2012) work altering temperature on settling plates in Hillarys Harbor, Australia gives insight to the potential effects of climate change on marine sessile communities. Although their settlement plates were submerged for only 36 days, Smale and Wernberg (2012) reported a significant increase of total average biomass and percent cover of an invasive tunicate on the heated plates. Despite being in a different ocean, this study revealed similar trends. The data from Smale and Werenberg (2012) and this study show the upper thermal limits of growth for the prolifically invasive species *Watersipora subtorquata*. Hillarys Harbor exhibited much higher maximum temperature (23-27^{o} C) than observed in Monterey Harbor (12-16° C). My results indicated a significant increase in the percent cover of *W. subtorquata* on the heated plates while Smale and Wernberg (2012) reported the opposite trends when they warmed their experimental plates by a similar degree (2.5°C). The thermal range of the optimal zone of *W. subtorquata* is likely to be between the heated treatment in my study and the control group of the Smale and Wernberg (2012).

The results of this experiment also support and differ from the findings of other studies on the role of temperature in recruitment and community development (Stachowicz *et al.* 2002, Sorte *et al.* 2010). Native and invasive species exhibited an earlier onset of recruitment in response to an increase in temperature in the Monterey harbor. This response does not fully align with the findings of Stachowicz *et al.* (2002) who only observed invasive species to exhibit these earlier and higher recruitment rates. Although some of the same species were looked at, the study of Stachowicz *et at.*

(2002) was in the more seasonal waters of the Northwestern Atlantic. Seasonality is known to affect reproduction and recruitment. For example, northern populations of the limpet *Patella aspera* undergo increased gonad production during the summer and experienced extended breeding periods when summer temperatures persisted longer than normal. Conversely, central and southern populations at lower latitudes spawn closer to the fall/winter when temperatures decrease. This difference in reproductive timing could be due to synchronization of reproduction with ambient thermal conditions (Lewis 1986). The reproductive pulse in Monterey Bay occurs because of the increase in average temperature following cessation of upwelling. Therefore, sustained ocean warming due to climate change is likely to induce earlier spawning seasons in organisms that inhabit the northern end of their range and possibly reduce the spawning season for species at the southern end of their native range. However, if future climate simulations prove correct about stronger coastal California upwelling conditions due to climate change (Synder *et al.* 2003) northern species at their southern thermal limit could experience longer spawning seasons. Either way, current spawning seasons will be altered if thermal changes persist.

Once settled, both native and invasive species grew faster, however the magnitude of the response was significantly higher in the invasive species group; a result similarly observed by Sorte *et al.* (2010) when temperatures were artificially increased in the laboratory for a sessile marine community in Bodega Bay, California. Still, the effects of thermal increase on an organism's physiology are not always uniform and the degree of the increase can prove harmful or lethal as seen with the Australian sea cucumber (*Australostichopus mollis)* when temperatures were increased 3-6°C (Zamora & Jeffs 2012).

When comparing this study to others, it is important to note the magnitude of the experimental warming. Many climate change studies subject their study species to more dramatic increases in temperature (Sorte *et al*. 2010, Zerebecki & Sorte 2011, Zamora & Jeffs 2012). Artificially increasing the temperature 3-6°C with no fluctuation to mimic natural thermal variability has its merits. These thermal changes can test the physiological limits of a species. Unfortunately, it is not clear if temperature increases of that magnitude are even realistic. Secondly, if climate change does cause global average sea temperatures to increase it will take decades to hundreds of years for that to occur. Experiments like the ones mentioned above completely remove transgenerational plasticity and a community's ability to adapt over time from consideration. The methodology used is this study is therefore more relevant because the heated plate system accounted for daily thermal fluctuations and also maintained a more subtle increase in temperature. Monterey Bay is likely to be highly localized with temperatures varying over short distances. A study conducted exploring intertidal temperature ranges between Southern California to Washington State showed a nonlinear latitudinal distribution of temperature (Helmuth *et al*. 2006). This thermal variability has a heterogeneous effect on an organisms' body temperature, which can promote or disrupt physiological functioning.

My results indicate that the invasive species in Monterey harbor benefited from increased substrate temperature. However, the harbor already contains the invasive species reported here, and no new invasions occurred. Nonetheless, the combination of a supply of propagules of new invasive species and changing environmental conditions presents a risk of establishment of new invaders (Lodge *et al.* 1993, Carlton 2000, Walther *et al.* 2009). This and previous studies (Stachowicz *et al.* 2002, Smale and

Wernberg 2012) predict increased abundance and diversity of invasive species in areas that are more prone to warming. Unfortunately, this prediction cannot be experimentally tested without deliberate introduction of new species. As models for local temperature change are developed this prediction can be tested.

It is also important to note the inherent bias of using any artificial substrate. The hardness, texture and chemical cues of a substrate can greatly affect which species settle (Wisely 1958, Barnes & Gonor 1973). There is also high variability in species' ability to settle on a specific substrate. Some organism's range of suitable recruitment substrate can be very narrow. For example, the encrusting bryozoan *Membranipora serrilamella* is only capable of settling on algae. Even though the kelp they recruit on was only a few hundred meters away from the study site, they were not a potential colonizer in this experiment. The nylon weave used as a settling surface in this study was chosen because it is sturdy, rugose, and more closely mimics current manmade infrastructures consisting of concrete and treated wood. However, the nylon weave may inhibit the recruitment of some organisms. In this study it was specifically intended to deter the proliferation of *Balanus sp.,* which are known to dominate hard and flat surfaces (Berntsson *et al.* 2000). The nylon surface successfully mimicked harbor substrate because the species that recruited during this experiment were representative of species that grow on harbor pilings and PVC settling tiles that were deployed prior to this experiment.

Successful invasive species are often eurythermic and better able to tolerate temperature change, perhaps the single most important adaptation in the context of climate change. The larger the temperature difference from average, the more stress that occurs on an organism's ability to maintain proper homeostatic functioning.

However, the loss of native species under predicted future conditions will not only be caused by direct temperature effects, but also through interspecific competition (Sorte *et al.* 2010). Therefore, if elevated temperatures persist, biological invasions will increase and displace native species. The processes by which native species will weaken or decrease in abundance are already in motion.

The data collected in this study allows for further understanding of the processes that are affected by rising ocean temperatures. Researchers will therefore be able to support better predictions on how local communities in the Monterey Harbor are affected by mild thermal increases and possible consequences of climate change. Aside from the capacity to negatively affect ecological systems, introduced species have already shown a great ability to damage vessels and marine infrastructure, costing governments and companies substantial revenue to repair. Harbor managers are already dealing with these consequences and these issues will only continue to worsen monetarily with increased temperatures due to climate change (Boyd 1972, Sorte *et al.* 2010). Preliminary studies like these allow for a potential invader to be identified and targeted. If the invader poses a substantial threat, further studies can be performed to combat the invader at a more focused effort. Gaining insight into potential ecological threats before they occur is an invaluable advantage if there is a need to combat an invader.

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